

# FRUITING PLANT ATTRACTIVENESS TO AVIAN SEED DISPERSERS: NATIVE VS. INVASIVE *CRATAEGUS* IN WESTERN OREGON

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## ABSTRACT

*Crataegus monogyna*, a hawthorn native to Europe, has successfully invaded much of North America since its introduction approximately 200 years ago. Successful dispersal by avian frugivores, relative to the native biota, may be one reason why *C. monogyna* is so invasive. To address this hypothesis I compared the attractiveness of *C. monogyna* and *C. douglasii suksdorfii* (the native hawthorn) to their primary dispersal agent (American robins) in western Oregon. A companion study in western Oregon (Sallabanks 1993) identified three *Crataegus* traits correlated with pome removal by robins: pome crop size, mean pome size, and mean pome pulp-to-pyrene ratio. With respect to these dispersal-related traits, *C. monogyna* was found to be superior to its native counterpart, producing larger displays of higher quality pomes. These results offer an explanation for the observed patterns of distribution and abundance of *C. monogyna* and *C. douglasii suksdorfii* at the study site specifically, and in western Oregon in general. To conclude I suggest possible recommendations for management against *C. monogyna* and for frugivorous birds.

Some animal-dispersed plants produce fleshy fruits as a nutritional reward to frugivores in exchange for seed dissemination (Howe 1986). The attractiveness of fruiting plants to frugivores plays an essential role in dispersal success and may have important implications for plant species invasion. Frugivorous mammals have significantly accelerated the invasion of the western United States by *Carpobrotus edulis* L. (Aizoaceae) (D'Antonio 1990). Birds were found to play an important role in the invasion of mediterranean-climate zone South Africa by *Acacia cyclops* A. Cunn. ex G. Don. (Mimosoideae) (Glyphis et al. 1981). Similarly, birds dispersed the seeds of *Myrica faya* Ait. (Myricaceae), enabling this species to colonize Hawaii (LaRosa et al. 1985; Walker 1990; Woodward et al. 1990).

In the western United States, the native hawthorn, *Crataegus douglasii* Lindl. var. *suksdorfii* Sarg. (Rosaceae), is restricted in its range from British Columbia to northern California, and east through Idaho to Montana (Hitchcock et al. 1961; Brunfield and Johnson 1990; T. A. Dickinson and R. M. Love personal communications). The invasive European hawthorn, *C. monogyna* Jacq., arrived in the United States in the early 19th century (Douglas 1914) and has

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since spread rapidly throughout much of North America, doing particularly well in the Pacific Northwest and the Great Lakes–New England regions. *Crataegus* is dispersed by producing polypyrenous pomes (fruits) to attract primarily avian frugivores (De Boer 1979; Courtney and Manzur 1985; Herrera 1987; Dickinson and Campbell 1991; Sallabanks 1992).

In this paper I focus on a study site in the Willamette Valley of western Oregon to examine differences in the dispersal potential between the native and invasive *Crataegus*. The results presented here may be applicable to other geographic regions; in Australia, for example, *C. monogyna* is expanding its range at a rate of 120 m/yr (Smith 1985) due to dispersal by birds (Mulvaney 1986; Bass 1989) and marsupials (Bass 1990). Specifically, I compare the attractiveness of both *C. monogyna* and *C. douglasii suksdorfii* (henceforth “*C. suksdorfii*”) to their primary dispersal agent, the American robin, *Turdus migratorius* L. In a companion study conducted at the same study site (Sallabanks 1993), it was determined which plant traits were correlated with the foraging choices of robins. Here I compare *C. monogyna* and *C. suksdorfii* with respect to these dispersal-related traits and discuss implications for the native and invasive species. More extensive data on fruiting and frugivory in the *C. monogyna*–*T. migratorius* system per se are documented elsewhere (Sallabanks 1992).

## METHODS

*Study site.* Field-work was conducted on the Nature Conservancy’s Cogswell-Foster Reserve in Linn County, western Oregon. *C. suksdorfii* is native to the Reserve, whereas *C. monogyna* was introduced approximately 100 years ago (Love and Feigen 1978) and now comprises approximately 70% of the *Crataegus* population (Love 1980). *C. suksdorfii* comprises only 10% of the *Crataegus* population, the remaining 20% being hybrids between the native and invasive *Crataegus* (Love 1980). At the study site, the only dispersers of *Crataegus* were robins. Cedar waxwings, *Bombycilla cedrorum* Vieillot, were occasionally observed flying overhead but rarely foraged; their role in the dispersal of *Crataegus* is therefore assumed to be negligible.

*Correlates of pyrene dispersal.* During the winters of 1989–1990 and 1990–1991, I monitored pome removal by robins from a large population ( $n > 200$ ) of fruiting *C. monogyna* plants at the study site. Several plant traits were also measured and then regressed against pome removal to determine predictors of pyrene dispersal rates. The methods used and results obtained are described in detail elsewhere (Sallabanks 1993). I limited my analyses to *C. monogyna* because

*C. suksdorfii* was not present in sufficient numbers and typically experienced negligible rates of pome removal (personal observation). In addition, the determination of which traits were correlated with the foraging choices of robins involved manipulating plants by removing pomes and entire branches. This kind of treatment for the already uncommon *C. suksdorfii* was considered unjustifiable.

*C. monogyna* vs. *C. suksdorfii*. In August 1990, in order to compare traits between the native and invasive *Crataegus*, I located all fruiting *C. suksdorfii* plants ( $n = 44$ ) at the study site and measured pome crop sizes by systematically counting the number of pomes on all branches. I then arbitrarily collected samples of approximately 20–50 pomes from each plant, and within 48 hours, drew 20 pomes from each sample for the following analyses. Each pome was measured in diameter and weighed to the nearest milligram. Pyrenes were then dissected from each pome, cleaned of pulp, and weighed. Knowing pome and pyrene weight, I calculated pulp weight and pulp-to-pyrene ratio. In addition, I recorded the number of pyrenes per pome. In September 1990, I located the majority of fruiting *C. monogyna* plants ( $n = 217$ ) at the study site and analyzed them for the same seven characters as for *C. suksdorfii*. For both *Crataegus* species, pomes were sampled on the first day that robins were observed feeding on them (*C. suksdorfii*, 18 August 1990; *C. monogyna*, 22 September 1990).

## RESULTS

*Correlates of pyrene dispersal.* The results presented here appear in more detail elsewhere (Sallabanks 1993); here I provide only what is relevant to the ensuing discussion. Three traits were found to be significantly and positively correlated with rates of pome removal from *C. monogyna* plants by robins at the study site: pome crop size, mean pome size, and mean pome pulp-to-pyrene ratio. Although pyrene dispersal per se was not measured, pome removal is a correlate of dispersal success; plants with larger pome crops, larger pomes, and pomes with higher pulp-to-pyrene ratios therefore had potentially higher rates of dispersal.

*C. monogyna* vs. *C. suksdorfii*. Six of the seven traits measured were significantly greater for *C. monogyna* compared with *C. suksdorfii* (Mann-Whitney U-tests; Table 1). Only the number of pyrenes per pome was significantly lower for *C. monogyna*. These results were typical of other years (personal observation; R. M. Love unpublished data).



TABLE 1. COMPARISON BETWEEN *C. MONOGYNA* AND *C. SUKSDORFII* FOR THE SEVEN TRAITS MEASURED. Values are means  $\pm$  SE.

	<i>C. monogyna</i> (N = 217)	<i>C. suksdorfii</i> (N = 44)	Mann-Whitney U-test	
			U	P
Pome crop size (pomes per plant)	2721 $\pm$ 301	1072 $\pm$ 203	3545.5	<0.025
Pome diameter (mm)	9.05 $\pm$ 0.06	7.89 $\pm$ 0.09	1114.0	<0.001
Pome weight (mg)	485.38 $\pm$ 7.20	276.13 $\pm$ 7.18	135.0	<0.001
Pulp weight (mg)	372.68 $\pm$ 6.48	191.06 $\pm$ 5.76	148.0	<0.001
Pyrene weight (mg)	112.76 $\pm$ 1.66	85.08 $\pm$ 2.85	1650.5	<0.001
Pulp-to-pyrene ratio	3.44 $\pm$ 0.06	2.39 $\pm$ 0.09	1446.0	<0.001
Number pyrenes per pome	1.02 $\pm$ 0.01	4.68 $\pm$ 0.05	0	<0.001

## DISCUSSION

*Attractiveness to dispersers: C. monogyna vs. C. suksdorfii.* Fruiting plants with larger fruit displays can achieve greater dispersal success for two reasons. Firstly, plants with large fruit displays are more conspicuous and are therefore more likely to be visited by frugivores (Snow 1971; Howe and Estabrook 1977). Secondly, frugivores may prefer to stay in plants with large fruit displays once they've found them because less time is wasted in search and travel; foraging is therefore more efficient (Martin 1985). *C. monogyna* bushes at the study site with larger pome displays were more likely to be visited by robins (Sallabanks 1992) and had a greater proportion of their pome crops removed (Sallabanks 1993). Differences in pome crop size between *C. monogyna* and *C. suksdorfii* (Table 1) may therefore lead to differences in robin visitation rates and fruit removal rates, and ultimately, pyrene dispersal rates. Similar results are reported by Knight (1986): alien fruiting species that are successful invaders of the south-western Cape of southern Africa, in general, have larger and more conspicuous fruit displays than many indigenous species.

Robins also consume a higher proportion of the pome crop from *C. monogyna* plants with larger pomes (Sallabanks 1993). Larger pomes contain more pulp compared with smaller pomes in both *Crataegus* species (Sallabanks 1992; unpublished data) and are therefore more nutritionally rewarding. Because *C. monogyna* pomes are larger than *C. suksdorfii* pomes (Table 1), they may therefore be preferred by robins. Furthermore, the pyrenes of *C. monogyna* are both larger and occur singly compared with those of *C. suksdorfii* (Table 1). Regurgitation of pyrenes or separation of pyrenes from pulp in the gut is therefore likely to be accomplished more efficiently for *C. monogyna* compared with *C. suksdorfii* (Levey and Grajal

1991; Murray et al. 1991). These factors suggest that *C. monogyna* pomes are more profitable to frugivores compared with those of *C. suksdorfii*.

Robins also prefer *C. monogyna* plants with higher mean pome pulp-to-pyrene ratios (Sallabanks 1993). The ratio of pulp-to-pyrene is a good approximation of pome profitability because it represents both the benefit in digestible pulp and cost in indigestible pyrene that a frugivore must consume (Howe 1986). From an energetic viewpoint, *C. monogyna* pomes are nearer the dispersers' optimum (high food : ballast ratio), whereas *C. suksdorfii* pomes are nearer the plants' optimum (low food : ballast ratio) (Herrera 1981). With respect to pulp-to-pyrene ratio, therefore, *C. monogyna* pomes are more attractive to dispersers compared with those of *C. suksdorfii* (Table 1).

*C. monogyna* and *C. suksdorfii* also differ in the color of ripe pomes; ripe pomes of *C. monogyna* are red, whereas those of *C. suksdorfii* are black. Although red pomes may be more conspicuous than black pomes, these color differences may not affect rates of pyrene dispersal. Most "bird-fruits" are red and/or black (Willson and Whelan 1990) and choice-tests with various *Turdus* species have found no consistent preferences for either color (Brown 1974; Willson et al. 1990; Murray et al. 1991).

Because *C. suksdorfii* pomes contain more pyrenes than those of their invasive counterparts (Table 1), it may be argued that any differences in attractiveness to frugivores are compensated for by increased pyrene dispersal per pome. Unfortunately for *C. suksdorfii*, however, often only one pyrene per pome contains a true seed (Dickinson and Campbell 1991). For *Crataegus* pomes to ripen, at least one pyrene must contain a seed; all *C. monogyna* pomes eaten by robins therefore contain seeds. In short, despite large differences in apparent seed number, seed dispersal per pome is probably quite comparable between the native and invasive *Crataegus*.

*Fruiting phenology.* An important aspect of seed dispersal, in addition to the production of attractive fruits, is the timing of fruit ripening (Thompson and Willson 1979). Rapid removal of ripe fruits is important for some summer and fall fruiting species because of a high probability of fruit destruction by invertebrates (Thompson and Willson 1978; Sallabanks and Courtney 1992). For instance, *Pyracantha coccinea* Roemer (Rosaceae) does well as an introduced species in the Mediterranean because it offers late ripening fruits at a period when other fruits are scarce (Debussche and Isenmann 1990).

Because *C. monogyna* and *C. suksdorfii* do not ripen synchronously, it is possible that fruit and frugivore phenology explain much of the variation in relative dispersal success. If phenology was the

only factor affecting dispersal success, however, then *C. monogyna* would be invasive only where it ripened without competition from native *Crataegus* ripening at the same time. This is not the case; many native *Crataegus* species ripen their pomes for dispersal during the fall and winter months in other parts of the United States where *C. monogyna* has also successfully colonized. Stiles (1980), for example, documents nine species of native *Crataegus* ripening their pomes in September and October in the eastern deciduous forest (i.e., at the same time as *C. monogyna*). Studier et al. (1988) also report that ripe pomes of the Washington hawthorn, *C. phaenopyrum* (L.f.) Med., are eaten by birds in February and March in Michigan.

*Implications for native biota.* While the results presented in this paper are by no means conclusive, they nevertheless offer an explanation for the observed patterns of distribution and abundance of *C. monogyna* and *C. suksdorfii* at the study site specifically, and in western Oregon in general. It is important to point out that traits which are shown to explain differential dispersal success in an intraspecific context may not necessarily be applicable in an interspecific context. Furthermore, efficient dispersal by frugivores may not be the only reason for the success of *C. monogyna*; other differences may exist between the native and invasive species (e.g., levels of seed predation, seedling performance and response to the successional mosaic, and/or demographic patterns). Clearly, future research must test the hypothesis established here by specifically examining the actual dispersal success of *C. suksdorfii* relative to *C. monogyna*.

Factors affecting species invasions are important to study because the native biota can be seriously affected. Invasive plants are known to compete with and, in some cases, locally threaten native species (e.g., this study; see also Mulvaney 1986; Braithwaite et al. 1989; de Rouw 1991), alter ecosystem development (Vitousek et al. 1987; Vitousek and Walker 1989), and change bird communities (Esler 1990; Fraser and Crowe 1990). Furthermore, hybridization can often occur between native and invasive species (e.g., *C. monogyna* and *C. suksdorfii* at the study site: Love and Feigen 1978). Such hybridization contaminates the gene pool of native taxa and therefore conflicts with one of the primary goals of conservation biology.

Finally, the results presented here can be used to make useful management recommendations in a number of ways. Where *C. monogyna* co-occurs with native *Crataegus* species, it is clear that the invasive is a potential threat and should be managed against. Alternatively, the promotion of a native species that could compete well with *C. monogyna* (but that would not cause problems for *C. suksdorfii*, for example) may serve to short-circuit the dispersal, and



therefore, the reproductive success, of the invasive. In contrast, for those parties interested in bird conservation, management for *C. monogyna* (via ornamental plantings, hedgerows, etc.) may lead to an increase in frugivore populations, although any such management must proceed with caution.

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